The Skull of *Stephanomys* and a Review of *Malpaisomys* Relationships (Rodentia: Muridae): Taxonomic Incongruence in Murids

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The cranial morphology of the extinct murid genus *Stephanomys*, previously known only by dental remains, is described here on the basis of partial skulls of three species of Pliocene age. Important cranial characters of the genus are a robust rostrum, a high zygoma, a wide zygomatic arch, a narrow interorbit, a large orbit, and an optic foramen in the backward position. In addition to some dental characters, *Stephanomys* shares most of these cranial traits with the extinct *Malpaisomys* from the Canary Islands. Some of these traits may be linked to the development of large eyes and life in a rocky environment. The peculiar dental pattern of *Stephanomys* (stephanodonty) is also present in some recent murids (*Oenomys* and *Thamnomys*) having a different skull morphology. A comparison with nine other extant genera of murids verified the relationship among *Malpaisomys*, *Stephanomys*, and *Acomys*, supporting our previous conclusion. Phenetic and cladistic analyses of 17 cranial and 23 dental characters show that skull morphology is phylogenetically informative but highly convergent and incongruent with other partial evidence based on dental and biochemical characters. The combined analyses of skull and teeth illustrate a case of mosaic evolution in murids.

KEY WORDS: Muridae; skull; dentition; phylogenetic analysis; mosaic evolution.

INTRODUCTION

The murid rodent genus *Malpaisomys* was described on the basis of fossils found in Lanzarote and Fuerteventura, Canary Islands (Hutterer *et al.*, 1988). Further research revealed that the genus became extinct about 800 years ago (Boye *et al.*, 1992) and that it had lived in these islands during the Upper Pleistocene (Michaux *et al.*, 1991). The phylogenetic relationships of this remarkable rodent have been discussed since its discovery. On the one hand, Hutterer *et al.* (1988), on the basis of 27 morphological characters, concluded that the genus was part of a monophyletic group including *Acomys* and *Uranomys*, which clustered with several extinct murines such as *Stephanomys*, *Occi-*

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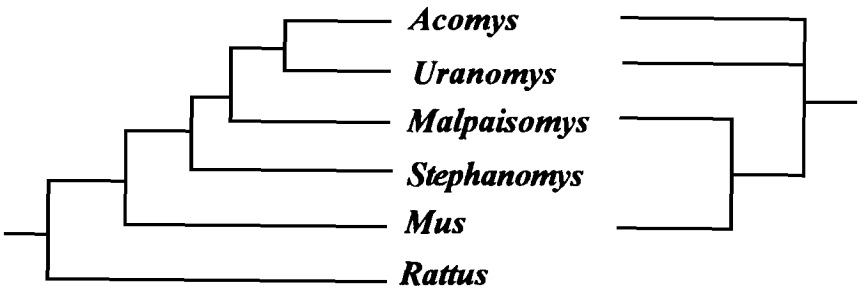


Fig. 1. Previous phylogenetic hypotheses on the relationships of *Malpaisomys*: left, according to Hutterer *et al.* (1988), right, according to Montgelard (1992).

tanomys, and *Paraethomys*, as well as extant *Grammomys* and *Oenomys*. The sister group of this clade was *Mus* (Fig. 1, left). On the other hand, Montgelard (1992), who studied the antibody reaction against albumin of four murid genera including bone extracts of *Malpaisomys*, concluded that *Malpaisomys* would cluster with *Mus* and not with either *Acomys* or *Uranomys* (Fig. 1, right).

In our first analysis, we compared the extinct *Malpaisomys* with seven extant rodent species from Africa and Europe. The inclusion of the nine extinct taxa was hampered by the usually fragmentary condition of the fossils; a few species were represented by fairly complete skulls (the subfossil *Canariomys*) but most were known from the dentition or isolated teeth only. An increase in our knowledge will therefore depend on the discovery of better-preserved fossils. Several extinct murids (*Stephanomys*, *Occitanomys*, and *Paraethomys*) are possibly related to *Malpaisomys* (Hutterer *et al.*, 1988). They are known by thousands of dental and fragmentary skeletal remains from Pliocene deposits of southwestern Europe and northern Africa and are especially abundant in samples from karstic fissure fillings. A partial skull of *Stephanomys* from Seynes was already present in the collections of the University of Montpellier. More partial skulls of two other species of *Stephanomys* were excavated by the authors in 1992 during joint fieldwork in Spain. This material allows us to describe, for the first time, the skull of representatives of the extinct genus *Stephanomys* and to test the two hypotheses on the phylogeny of *Malpaisomys*.

Stephanomys appeared in the Late Miocene of southwestern Europe (Michaux, 1971; Van de Weerd, 1976) (see Fig. 2). In the Latest Miocene its distribution had extended to Italy (De Giuli, 1989) and North Africa (Coiffait *et al.*, 1985). During the Pliocene its distribution was limited to southwestern Europe. The latest known *Stephanomys* has a Late Pliocene age (Gmelig Meyling and Michaux, 1973). Eighteen species of *Stephanomys* have been named so far, some of which are formally not available (see Appendix).

We included in our comparison several extant genera of murids sharing some special characters with the extinct ones, in order to evaluate the distribution of homoplasies and homologies of cranial and dental characters. *Oenomys* and *Thamnomys* are herbivorous murids having stephanodont upper molars like *Stephanomys* (see below); *Stenocephalemys* has a narrow interorbital region resembling *Malpaisomys*; *Lophuromys* has previously been discussed as being closely related to *Acomys* (Chevret *et al.*, 1993b),

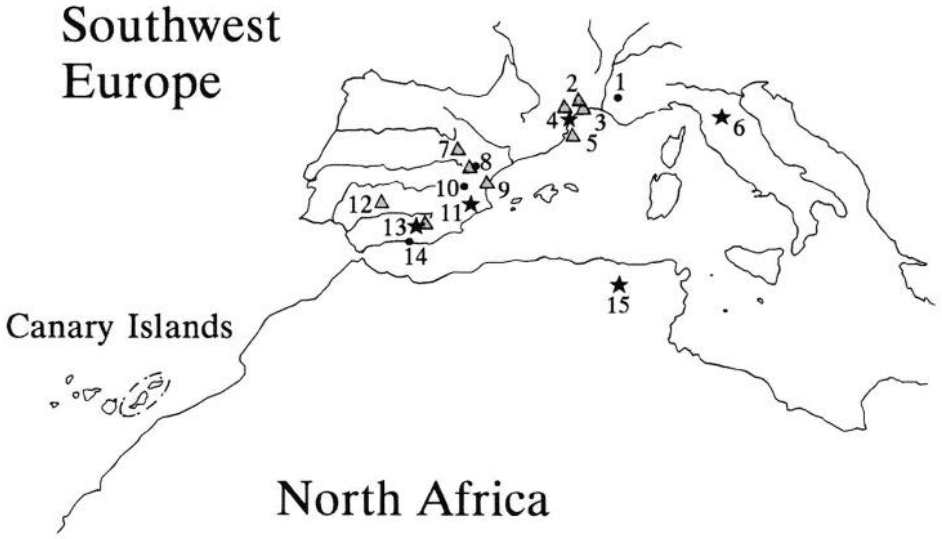


Fig. 2. Distribution of main localities for *Stephanomys* in the Mediterranean region. Circles, Late Miocene; stars, Latest Miocene–Earliest Pliocene; triangles, Pliocene. (1) Cucuron; (2) Seynes; (3) Sête-Balaruc; (4) area of Perpignan, Pyrénées Orientales; (5) Islas Medas; (6) Brisighella; (7) Layna; (8) area of Teruel; (9) Casablanca; (10) Venta del Moro; (11) Alcoy; (12) area of Córdoba; (13) area of Granada; (14) Salobreña; (15) Argoub Kemellal. The distribution of *Malpaisomys insularis* during the Pleistocene and Holocene in the Canary Islands is shown by the dashed oval.

which was related to *Malpaisomys* (Hutterer *et al.*, 1988); *Otomys* is an example of a highly specialized herbivorous murid; and *Mastomys* and *Dasymys* represent rather generalized skull morphologies for Murinae. *Deomys* belongs to a different subfamily [Dendromurinae or Deomyinae (see Denys *et al.*, 1995)] and was tested as a possible outgroup. *Mus* and *Rattus* are also included in the comparison because the *Rattus–Mus* dichotomy is a general reference for the calibration of molecular clocks. Paleontologists have recognized this dichotomy early in the phylogeny of the murids and dated it at ca. 10 My (Jacobs, 1978; Jaeger *et al.*, 1986; Jacobs *et al.*, 1989). The taxonomy based on dental characters in the murids has been challenged by biochemical data (Chevret *et al.*, 1993b; Denys *et al.*, 1995). Here we test the taxonomic congruence (*sensu* Mickevitch, 1978) and the conflicting phylogenetic hypotheses for murids using cranial and dental characters separately and combined.

MATERIALS AND METHODS

Skulls of *Stephanomys* Schaub, 1938 were collected from karstic fissure fillings of Pliocene age in southern France and Spain: *S. donnezani* (Déperet, 1890) from the Middle Pliocene of Layna [Soria, Spain (Crusafont *et al.*, 1969)], *S. thaleri* n. sp. renaming of *S. "thaleri"* Cordy, 1976, *nomen nudum* from the Late Pliocene of Seynes [Gard, France (Michaux, 1965)], and *S. balcellsi* Gmelig Meyling and Michaux, 1973 from the Late Pliocene of Casablanca [Castellon, Spain (Esteban Aenlle and López-Martínez, 1987)]. The fossils are deposited in the collections of the Departamento de

Paleontologia, Universidad Complutense de Madrid (UCM), in the Laboratoire de Paléontologie des Vertébrés, Université Montpellier II (UM), and in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK).

All skulls of extant Muridae used for comparison were taken from the collections of the Museum Alexander Koenig in Bonn, with the exception of a skull of *Stenocephalemys* loaned by the Staatliches Museum für Naturkunde, Stuttgart. Dental characters were also examined in the collections of the Muséum National d'Histoire Naturelle, Paris.

Genera and species retained for the phylogenetic study and their respective codes used for the analyses are listed below. The authors and the years of description of all the species listed (except for *Stephanomys*) are given by Musser and Carleton (1993).

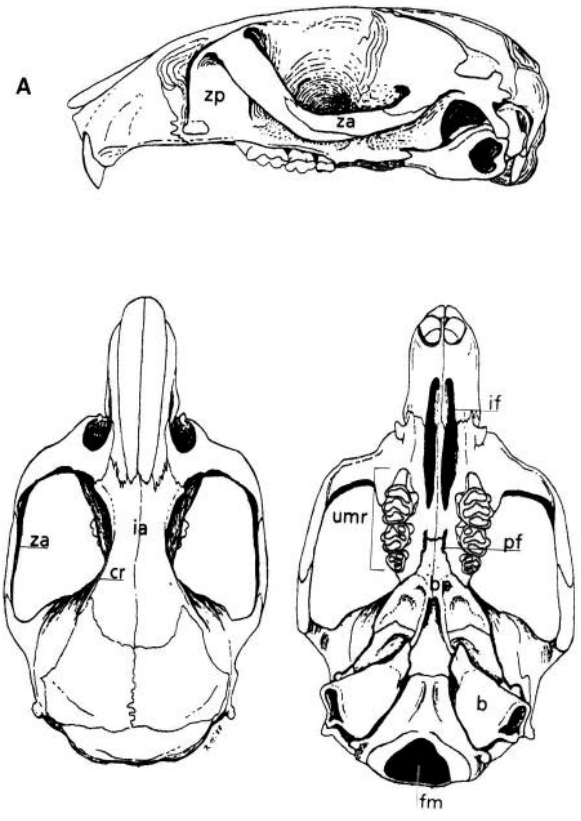
ACO	*Acomys* (*A. dimidiatus*)
DAS	*Dasmys* (*D. rufulus*)
DEO	*Deomys* (*D. ferrugineus*)
LOP	*Lophuromys* (*L. flavopunctatus*)
MAL	*Malpaisomys* (*M. insularis*)
MAS	*Mastomys* (*M. verheyeni*, *M. peregrinus* = *M. erythroleuceus*).
MUS	*Mus* (*M. musculus*)
OEN	*Oenomys* (*O. hypoxanthus*)
OTO	*Otomys* (*O. irroratus*)
RAT	*Rattus* (*R. rattus*)
STE	*Stephanomys* (*S. donnezani*, *S. thaleri* n. sp., *S. balcellsi*)
STN	*Stenocephalemys* (*S. griseicauda*)
THA	*Thamnomys* (*T. kempi*)

In a preliminary analysis, we also included species of *Arvicanthis*, *Canariomys*, *Dendromus*, *Lamottemys*, *Malacomys*, and *Pelomys*. For the test of the two conflicting hypotheses (see Fig. 1) they are not relevant and have thus been excluded. We describe below the cranial and dental characters used for the systematic analyses. For the nomenclature of the skull and teeth, see Fig. 3.

RESULTS

The formal taxonomy of *Stephanomys* Schaub, 1938 is in need of revision. Fifteen specific names have been published (see Appendix). Several names have been proposed in unpublished manuscripts and nevertheless used by other authors in print. One of these invalid names is validated here as *Stephanomys thaleri* n. sp.

Fig. 3. (*Opposite*) (A) Cranial features, based on a skull of *Malpaisomys*. b, bulla; bp, bony palate; cr, cranial ridge; fm, foramen magnum; ia, interorbital area; if, incisive foramina; pf, palatal foramina; umr, upper molar row; za, zygomatic arch; zp, zygomatic plate. (B) Dental features, based on the dentition of *Stephanomys*. Terminology for the dentition according to Musser and Newcomb (1983). Left, upper M1/-M3/; right, lower m/1-m/3. a-cen, anterocentral cusp; a-lab, anterolabial cusp; a-ling, anterolingual cusp; ed, entoconid; hd, hypoconid; lcm, labial cingulum; md, metaconid; pd, protoconid; pc, posterocingulum; plc, posterolingual cingulum; t1-t8, tubercles 1 to 8.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Stephanomys thaleri n. sp.

Synonyms: *Stephanomys balcellsi* Villalta, 1965 in Gmelig Meyling and Michaux, 1973, p. 1442, Pl. 1, Fig. 13; *Stephanomys thaleri* Cordy, 1976 in Aguilar *et al.*, 1993 p. 7, Pl. 1, Figs. 13 and 14.

Type locality: Seynes, Gard, France.

Age: Late Pliocene.

Derivatio nominis: We follow the suggestion of Cordy (1976) to name the species in honor of Professor Louis Thaler from Montpellier University.

Holotype: Right lower molar series, UM 47 (length m1–m3 = 7.21 mm; length m1 = 2.74; width m1 = 1.83), in the collections of the Laboratory of Palaeontology, University of Montpellier II (Fig. 14).

Additional material: partial skull collected by J. Michaux from Seynes (Gard) (Figs. 6, 7, and 8, middle).

Diagnosis: *Stephanomys* of rather large size; molars showing complete stephanodonty; crown relatively high. M1 and M2 having t4 with distinct distal spur. M2 having t1 with well-developed mesial spur. Labial cingulum of m1 and m2 well differenciated, not well connected to protoconid. Posterior cingulum of m1–m2 round-shaped and large, arising from the entoconid side.

Distribution: Late Pliocene of southern France and Spain.

Comments: For a discussion of the evolution of the species, see Cordy (1978), Bachelet and Castillo Ruiz (1990), Aguilar *et al.* (1993), and Renaud *et al.* (1996).

The *Stephanomys* population from Layna has been attributed to different species. Here it is named *S. donnezani* according to Crusafont *et al.* (1969), since no thorough revision of the genus has been made so far. The *Stephanomys* population from Casablanca has been attributed to *S. "progressus"* Cordy by Renaud *et al.* (1996), a *nomen nudum*. This name was used in the unpublished thesis of Cordy (1976) to distinguish the *Stephanomys* population of Cordoba from that of the Islas Medas, which is the type locality of *Stephanomys balcellsi* Gmelig Meyling and Michaux, 1973. Here the *Stephanomys* population from Casablanca is assigned to *Stephanomys balcellsi*; we agree with Gmelig Meyling and Michaux (1973) and with Ruiz Bustos (1986) in that the populations of the Islas Medas and Cordoba belong to the same species.

Skull Characters

Some skull characters commonly observed in anatomical descriptions have been used without further explanation. In addition, we have used characters proposed by Musser and Newcomb (1983), Carleton and Musser (1989), and Musser and Heaney (1992) (characters 7, 10, 12). Some of the character definitions have been modified by us (characters 1, 4, 5, 6, 8). Other characters are newly proposed here (characters 2, 3, 9, 11, 13–17). The polarity of the new characters has been established using the most widespread state as primitive. The analyzed cranial characters are defined as follows.

Character 1: Shape of the Zygomatic Plate and Notch

Carleton and Musser (1989, Fig. 14) defined this character and recognize three states. A fourth state has been added. They are defined as follows. 0: Plate narrow,

notch indistinct. 1: Intermediate state. Notch distinct but shallow. 2: Plate broad. Notch well incised. 3: Anterior part of plate concave. Notch well incised. The four states may be interpreted as steps in a morphocline with a linear polarity from the most primitive state (0) to the most derived one (3).

Character 2: Shape of the Infraorbital Canal

This character needs to be observed in frontal view of the skull. The different states of this character are illustrated in Fig. 4. The most widespread state, interpreted as the primitive one, is intermediate between the two other states, which would be divergent from it. States are defined in frontal view. 0: Triangular shape. 1: Ovoid. 2: Rectangular.

Character 3: Orientation of the Upper Zygomatic Arch

This character can be observed in a frontal view of the skull. The two character states are illustrated in Fig. 4. 0: The upper zygomatic branch forms an angle with the platform-shaped skull roof (platform shape; Fig. 4, top and middle). 1: The upper zy-

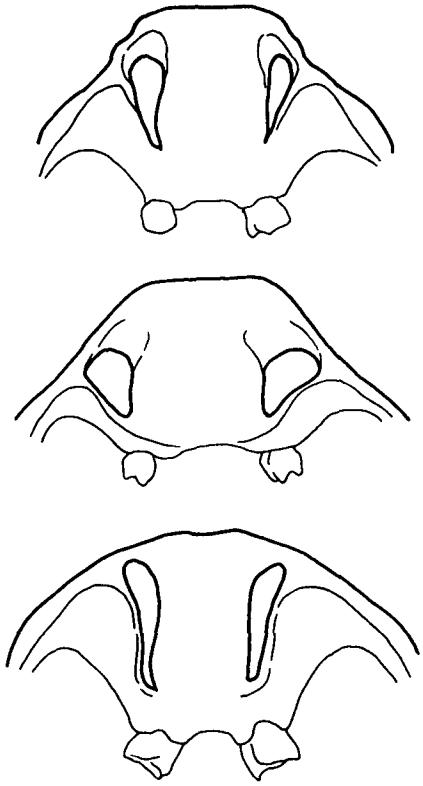

Fig. 4. Schematic anterior view of crania to show the orientation of the upper zygomatic arch and shape of the infraorbital canal. Top, *Arvicanthis*; middle, *Lophuromys*; bottom, *Stephanomys*.

gomatic branch forms a continuous bow with the skull roof (umbrella shape; Fig. 4, bottom). The primitive state may correspond to the most widespread condition.

Character 4: Interorbital Area and Cranial Ridges

This character has been defined by Musser and Heaney (1992, Fig. 60). We have added an intermediate state. States are as follows. 0: Interorbit symmetrically constricted (hour-glass shaped). Margin of the dorsal cranium smooth. 1: Interorbit symmetrically constricted. Dorsal cranium with ridges running from back, over the orbital roof, to the front, medially to the orbit wall. 2: Asymmetric interorbit. Thick crests cover the orbit margin and converge in the anterior part of the interorbit.

Character 5: Size of the Incisive Foramina

The size of the incisive foramina relative to the diastema presents the following character states: 0, considerably shorter than diastema; 1, long, filling most of the space of the diastema. An illustration of these conditions is given by Musser and Newcomb (1983; Fig. 93, p. 539, for state 0; Fig. 64D, p. 483, for state 1).

Character 6: Position of the Incisive Foramina

In addition to the two states distinguished by Musser and Newcomb (1983), we define another state in which the foramina terminate far in front of the molars. Conditions 1 and 2 would be independently derived. Definitions of states are as follows: 0, terminating near the level of the first molars; 1, terminating backward between the molar rows; 2, terminating far in front of the molars.

Character 7: Pterygoid Fossa

Some murid rodents exhibit a flattened pterygoid area, which seems to be a primitive state. The deep pterygoid fossa commonly found in modern Murinae would be a derived state. Definitions of states are as follows: 0, pterygoid bone flat or forming a shallow fossa; 1: deep pterygoid fossa.

Character 8: Bony Palate

Musser and Newcomb (1983, p. 535) distinguish two states in this character, also called the palatal bridge. We recognize another derived state, where the bony palate ends anterior to the distal border of the third molar. The polarity would be divergent in the two derived states. Definitions of states are as follows: 0, bony palate terminates near to the posterior borders of the third molars (Musser and Newcomb, 1983, Fig. 97, p. 549); 1, bony palate ends anterior to the distal border of the third molars (Musser and Newcomb, 1983, Fig. 93, p. 539); 2, bony palate extends considerably backward, far beyond the third molars (Musser and Newcomb, 1983, Fig. 5, p. 338; Hutterer *et al.*, 1988, Fig. 4).

Character 9: Size of the Posterior Palatal Foramina

Two states are recognized; the primitive state is the condition with small foramina. States are defined as follows: 0, short, foramen nearly as long as wide; 1, long, clearly longer than wide.

Character 10: Position of the Posterior Palatal Foramina

According to Musser and Heaney (1992, Fig. 60), two stages can be recognized: 0, the foramina are situated anterior to or on the maxillopalatine suture; 1, the foramina are shifted backwards, the suture passing anterior to them.

Character 11: Orientation of the Tooth Rows

Some murids show a divergent orientation of the tooth rows, which appears to be a derived specialization, compared with the parallel tooth rows commonly found. States are as follows: 0, parallel oriented; 1, clearly divergent, tapering backward.

Character 12: Bullae

Carleton and Musser (1989, Fig. 18) and Musser and Heaney (1992, Fig. 61) describe and interpret the polarity of this character, which is defined as follows: 0, the flange of the petrosal bone extends forward, building the medial wall of the carotid canal; 1, the petrosal bone is not so extended, with the carotid canal built by the ectotympanic bone. In Fig. 5, some undescribed bullae of *Malpaisomys*, *Stenocephalemys*, *Mastomys*, and *Acomys* are shown.

Character 13: Size of the Stapedial Foramen

A very small stapedial foramen (Fig. 5) is sometimes present, which we consider to be derived, compared with the larger-sized stapedial foramen usually found in most Muridae. Moreover, the small size of the stapedial foramen has been linked to a derived cephalic arterial system by Carleton and Musser (1989) and Musser and Heaney (1992). The states are as follows: 0, size large, as big as carotid canal; 1, size clearly smaller than carotid canal.

Character 14: Angle of the Temporal Apophysis

The temporal apophysis and the squamosal bone form an angle which may be variable. A right angle is considered as a derived trait and the frequently observed narrow angle may be primitive. The states are as follows: 0, temporal zygomatic apophysis forms a narrow angle with the braincase; 1, apophysis begins nearly at a right angle (as in Fig. 3A, dorsal view).

Character 15: Ventral Branch of the Zygomatic Plate

In *Deomys* the ventral branch of the zygomatic plate originates at the level of the first upper molar. This is considered to be the primitive state of the character. Two states are defined as follows: 0, ventral branch of the zygomatic plate at the level of M1/; 1, ventral branch anterior to M1/.

Character 16: Shape of the Foramen Magnum

The shape of the foramen magnum in occipital view may be either round or clearly oval, being wider than high. The former state is frequently observed in Muridae and is considered as primitive. The states are defined as follows: 0, round, nearly circular in shape; 1, wider than high.

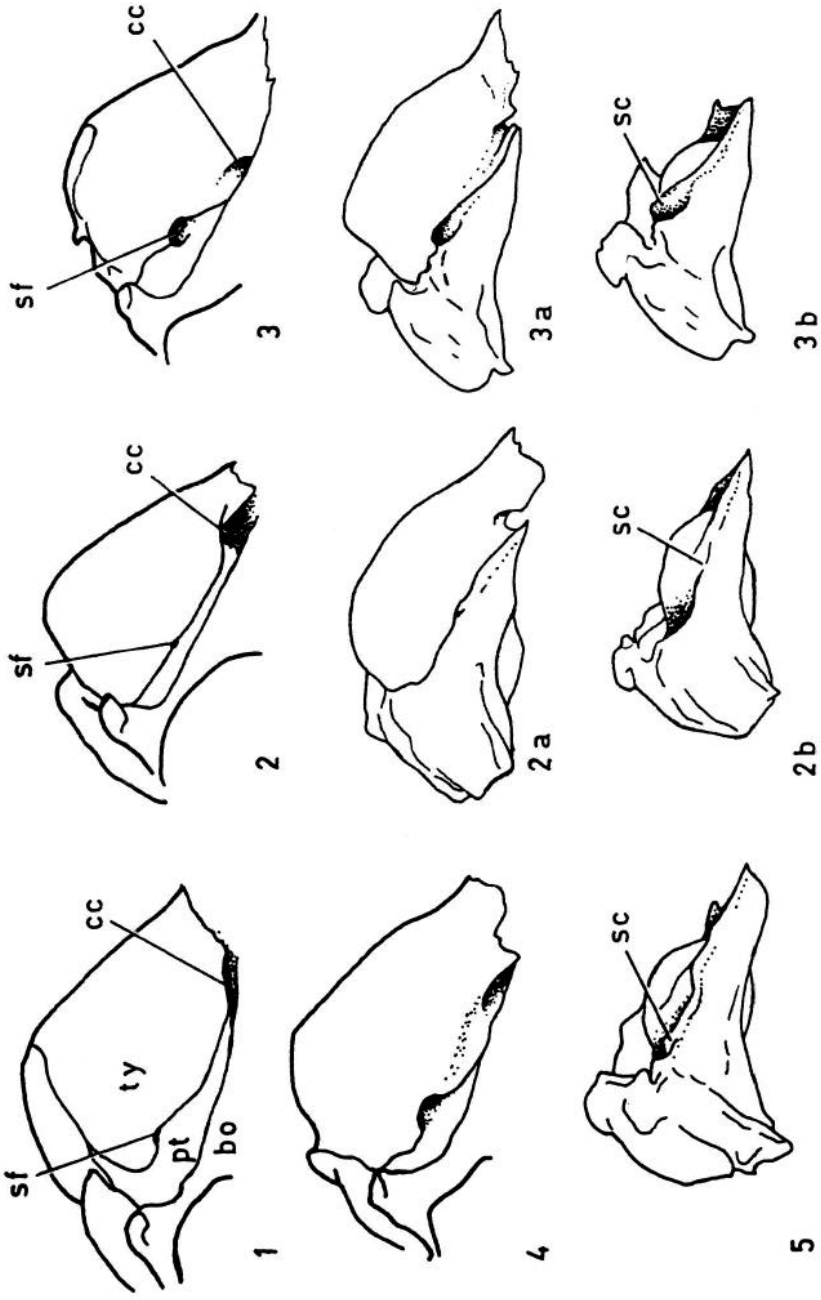

Fig. 5. Ventral view of the auditory bulla or the petrosal bone in some recent and fossil murids. 1, *Acomys*; 2, *Malpaisomys* (2, complete; 2a, isolated bulla; 2b, isolated petrosal bone); 3, *Mastomys* (*idem* 2); 4, *Stenocephalemys*; 5, *Stephanomys* (*S. balcellsi*, Casablanca). bo, basioccipital; cc, carotid canal; pt, petrosal bone; sc, stapedial canal; sf, stapedial foramen; ty, tympanic bone.

Character 17: Position of the Optic Foramen

In lateral view the position of the optic foramen may be posterior to the last molar or not. The derived state would be the posterior position. The states are defined as follows: 0, at the level of the third molar (Fig. 9B); 1, clearly behind the third molar (Figs. 8 and 9A).

Dental Characters

Dental characters are taken from Hutterer *et al.* (1988) and from Denys *et al.* (1992, 1995). Some of them have been slightly modified. They are defined as follows (see Fig. 3).

Character 1: General morphology of the crown: 0, brachyodont; 1, semihypsodont.

Character 2: Enamel thickness different at the front and rear faces of the cusps: 0, thickness of enamel slightly differentiated; 1, relatively undifferentiated; 2, strongly differentiated. The two derived states have probably evolved independently.

Character 3: Number of roots on M1/: 0, fewer than 5; 1, 5 or more.

Character 4: Lingual cusps on M1/: 0, anterolingual cusp (t1) absent; 1, present.

Character 5: Position of the cusp t1 on M1/: 0, in a backward position relative to t3 as in *Acomys* and *Stephanomys*; 1, intermediate as in *Apodemus*; 2, situated at the level of t3 as in *Dasymys*. States 0, 1, and 2 represent a morphocline.

Character 6: Accessory cusp (t1 bis) between t1 and t2 on M1/: 0, absent; 1, present.

Character 7: Connection of t1 with t2 on M1/: 0, present; 1, absent.

Character 8: Cusps t2–t3 and t5–t6 on M1/: 0, connected but clearly individualized; 1, fused.

Character 9: Connection of t6 with t9 on M1/: 0, absent; 1, variable; 2, present. States 0, 1, and 2 represent a morphocline.

Character 10: Connection between t1 and t5 on M1/: 0, absent; 1, incomplete; 2, present. States 0, 1, and 2 represent a morphocline.

Character 11: Connection between t3 and t5 on M1/. States as in character 10.

Character 12: Cusp t4 on M1/: 0, without posterior crest; 1, variable; 2, with a posterior crest.

Character 13: Posterior cingulum on M1/: 0, large; 1, small; 2, absent. States 0, 1, and 2 represent a morphocline.

Character 14: Anterocentral cusp on m/1: 0, absent; 1, sometimes present; 2, always present. States 0, 1, and 2 represent a morphocline.

Character 15: Labial cingular margin on m/1: 0, with few accessory cusps; 1, without cusps; 2, with many accessory cusps. The two derived states, 1 and 2, have probably evolved independently.

Character 16: Posterior cingulum on m/1: 0, large; 1, small; 2, absent. States 0, 1, and 2 represent a morphocline.

Character 17: Anterolophid on m/1: 0, isolated from the second pair of main cusps as in *Rattus*; 1, narrow connection between anterolophid and anterior main cusps; 2, wide connection as in *Mus*. States 0, 1, and 2 represent a morphocline.

Character 18: Connection between the median and the posterior pairs of main cusps on m/1: 0, absent; 1, variable; 2, present.
Character 19: Anterolabial cusp on m/2: 0, large; 1, reduced or absent.
Character 20: Cusp t3 on anterolabial side of M2/: 0, present; 1, absent.
Character 21: Cusp t1 on anterolingual side of M2/: 0, absent; 1, present.
Character 22: Cusp t3 on anterolabial side of M3/: 0, present; 1, absent.
Character 23: Cusp t1 on anterolingual side of M3/: 0, absent; 1, present.

The phylogenetic importance of the two latter characters on M3/ has been recognized before by Petter (1983); we therefore propose to call them "Petter's characters" here. Their significance has been confirmed by Denys and Michaux (1992).

For the systematic analyses, we have first treated the cranial and dental characters separately (partial evidence), and then combined them (combined evidence), in order to test for phylogenetic congruence (Hillis, 1987; Rieppel, 1989; Kluge and Wolf, 1993).

The phenetic analyses of global similarity using the Fitch–Margoliash algorithm were performed with the help of a PHYLIP computer package (Felsenstein, 1987), and the phylogenetic analyses were conducted with the aid of the programs PAUP (Swofford, 1990) and HENNIG86 (Farris, 1988). The characters were first given as unordered using binary definitions (presence–absence), then ordered using multistate definitions, according to the polarities discussed above, based on previous studies (Musser and Newcomb, 1983; Carleton and Musser, 1989; Musser and Heaney, 1992) and on our own observations. The outgroup was selected either using the Lundberg and the Midpoint methods (Swofford, 1990; Nixon and Carpenter, 1993) or by inserting an hypothetical ancestor having all primitive character states (Farris, 1988).

THE SKULL OF *Stephanomys* AND A COMPARISON WITH *Malpaisomys*

Rostrum

The rostrum of *Stephanomys* shows some differences when the three species are compared (Figs. 6–9). Those of *S. donnezani* and *S. thaleri* are slender and rather long, as in many other murids such as *Rattus* and *Mastomys* (Table I). That of *S. balcellsi* is relatively stouter. Nasals are broad in the anterior part and gradually taper backward; conversely, the dorsal part of the premaxillary bones is thinner in the front and broader in the back. In lateral view, the rostrum of *S. donnezani* is relatively lower than in *S. thaleri* and *S. balcellsi*; the robust aspect of the rostrum of the latter species is similar to that of *Dasymys*. The incisors are preserved in some specimens, showing that they were not grooved.

Zygomatic Region

The zygomatic arches are wide. In dorsal view (Fig. 6), *Stephanomys* has conspicuous zygomatic notches, as in other Murinae. The development of the notch in *Stephanomys donnezani* is relatively larger than in other Murinae. It is even larger in *S. balcellsi*, and *S. thaleri* from Seynes has the widest notch.

The skull of *Stephanomys* shows remarkably high and wide zygomatic plates, which reach nearly the dorsal margin of the skull. The upper root of the zygomatic arch and

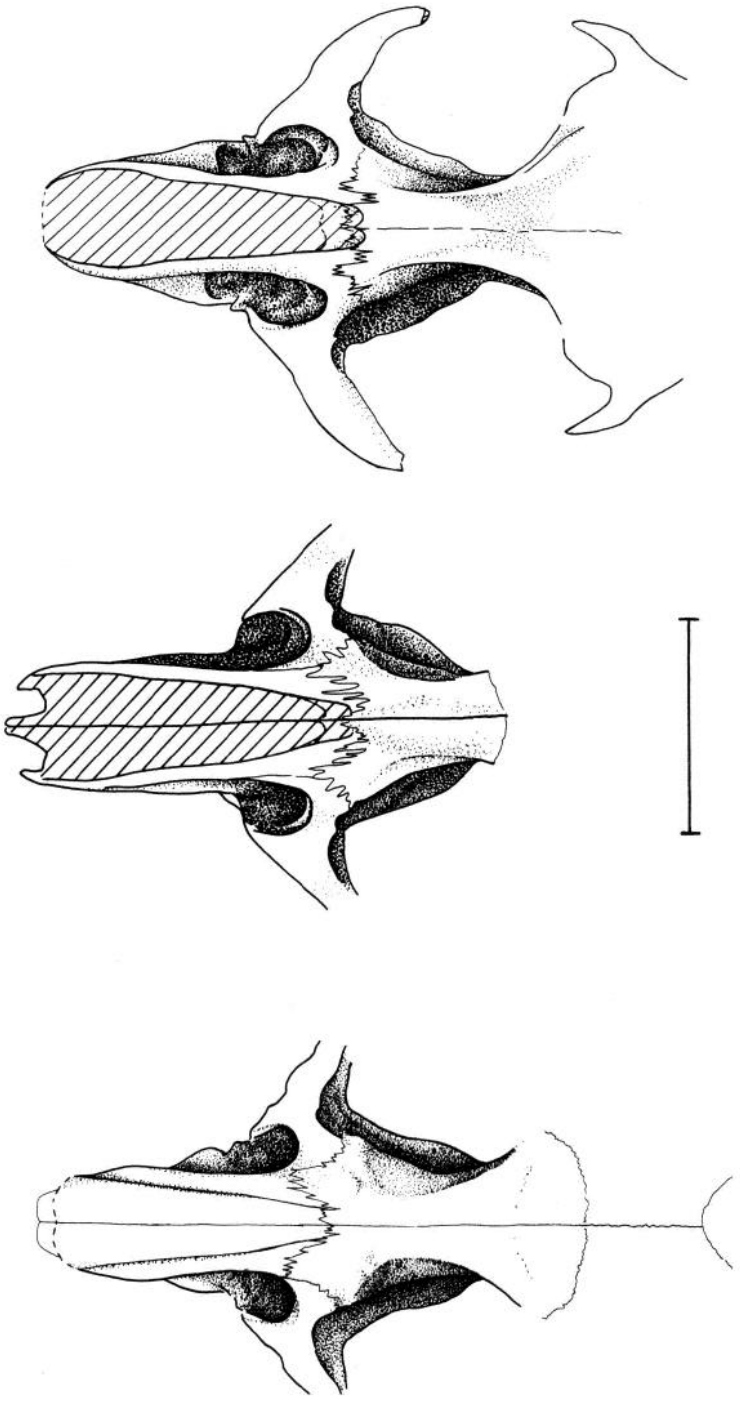

Fig. 6. Skulls of *Stephanomys* in dorsal view. Left, *S. donnezani*; middle, *S. thaleri*; right, *S. balcellsi*. Hatched region indicates broken part of skull. Scale is 10 mm.

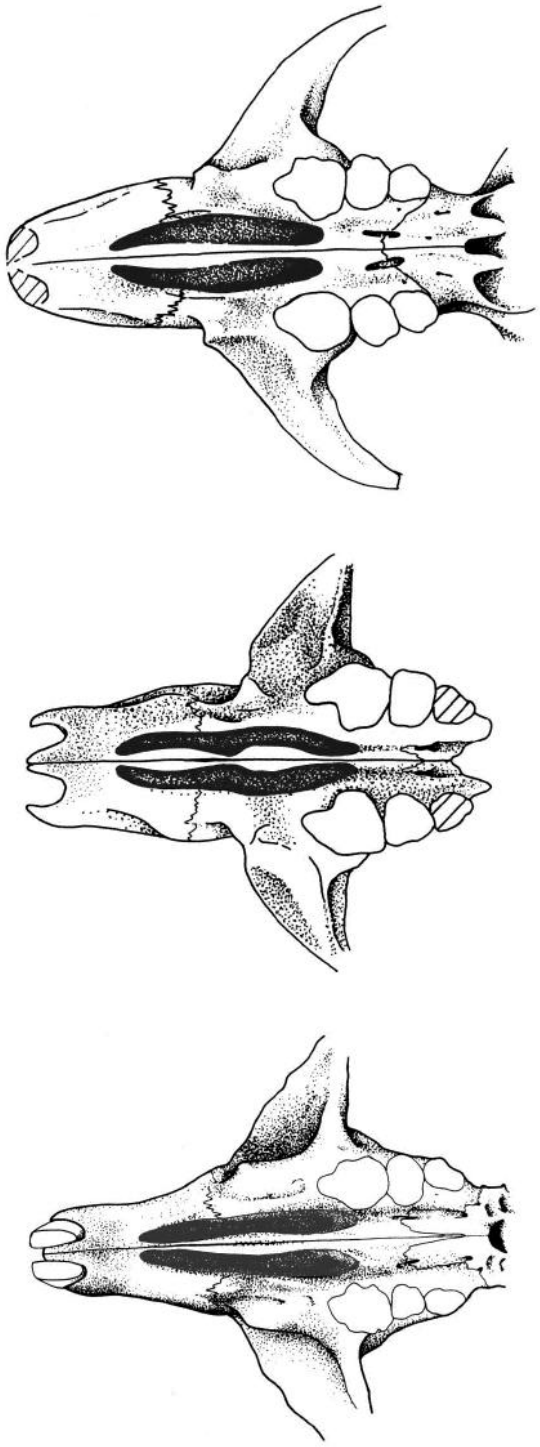

Fig. 7. Skulls of *Stephanomys* in ventral view (same specimens as in Fig. 6).

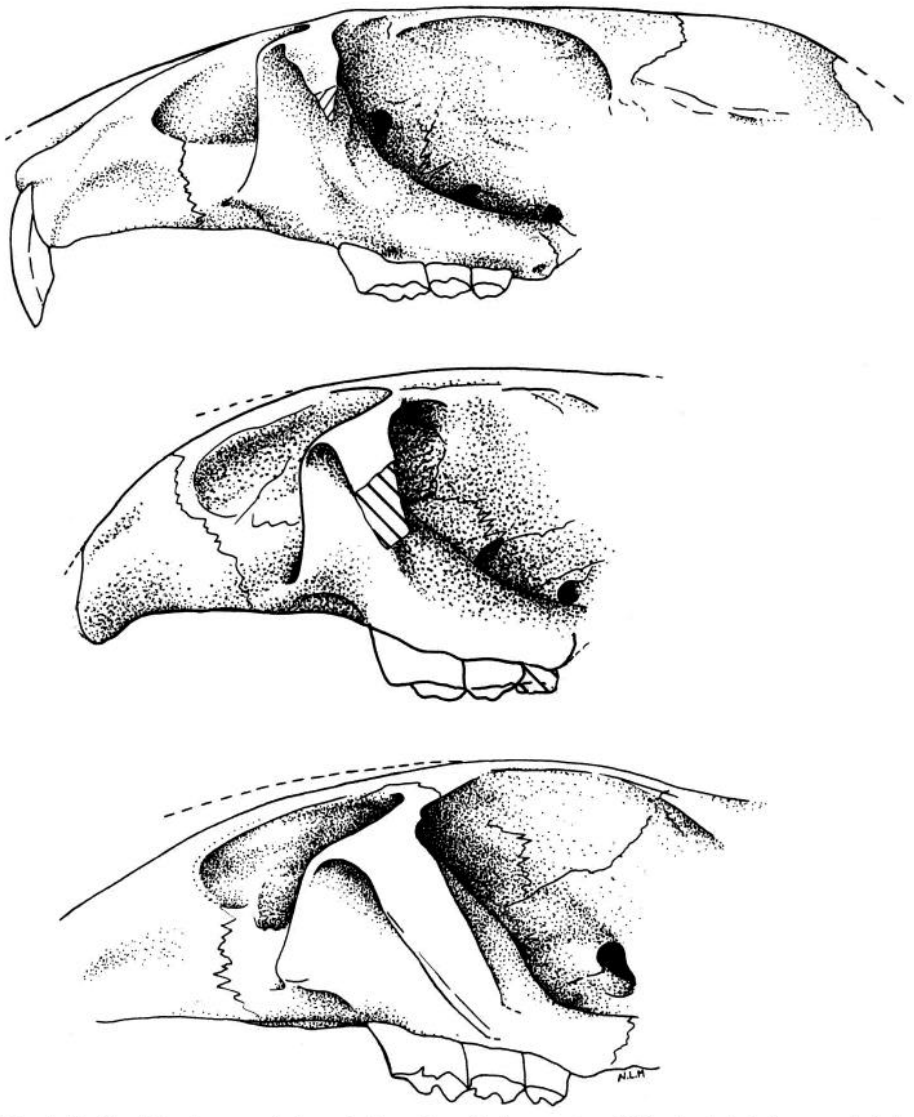

Fig. 8. Skulls of *Stephanomys* in lateral view. Top, *S. donnezani*; middle, *S. thaleri*; bottom, *S. balcellsi*. Same specimens as in Fig. 6.

the dorsal roof of the skull form an umbrella-shaped bow in frontal view (Fig. 4, bottom). We found this condition to be rare in Murinae, where the upper zygomatic branch is positioned lower in relation to the dorsal roof of the skull and does not form an umbrella but a platform (Fig. 4, top and bottom). Only the Canarian endemic genus *Malpaisomys* shows this umbrella-shaped skull.

In lateral view (Fig. 8), the anterior margin of the zygomatic plate in *S. balcellsi*

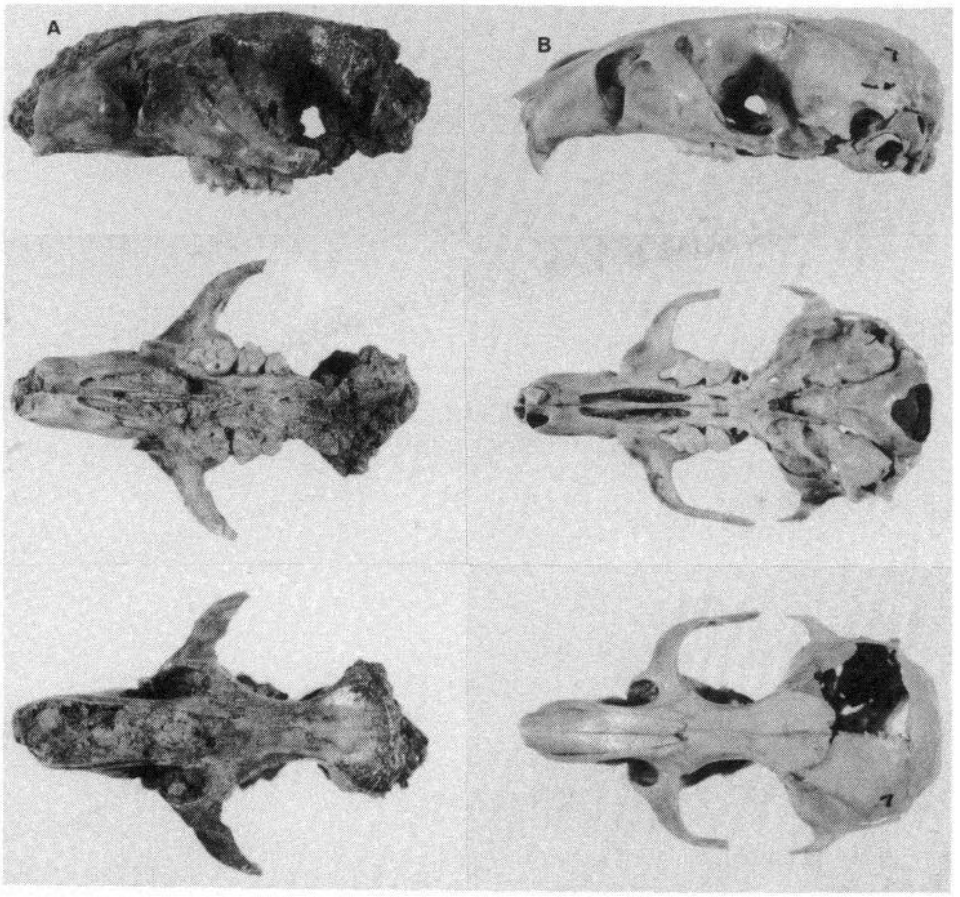

Fig. 9. Partial skull of *Stephanomys balcellsi* from Casablanca (A), in lateral, ventral, and dorsal views (UCM, CAS NI6MU085), and skull of *Malpaisomys insularis* from Fuerteventura (b), in lateral, ventral, and dorsal views (ZFMK Can01).

Table I. Comparison of the Skull Characters of the Three Studied *Stephanomys* Species (See Figs. 6–8)

Character	*S. donnezani*	*S. thaleri* n. sp.	*S. balcellsi*
Rostrum	Slender, long, low	Slender, long, high	Stout, high
Zygomatic notch	Large, wide	Very large, wide	Very large, narrow
Anterior margin of the zygomatic plate	Vertical, high	Vertical, intermediate	Oblique, low
Anterior part of the maxillary bone	Thick, not covering foramina	Intermediate	Very thick, covering foramina

is obliquely directed to the ventral face of the snout. The profile is nearly vertical in *S. donnezani* from Layna and *S. thaleri* from Seynes. The surface of the zygomatic plate is concave, with its lateral and posterior walls nearly vertical, forming a deep fossa for the insertion of the anterior masseter muscle.

The ventral branch of the zygomatic plate originates at the level of the first molar in the three species studied. *Malpaisomys* and *Deomys* exhibit a similar condition. This character is different in most extant Muridae, where the ventral branch begins usually in front of the anterior root of the first molar. The temporal apophysis of the zygomatic arch could be observed in some isolated pieces of the squamosal bone. The apophysis forms a wide angle with the squamosal plate in the posterior part of the orbit. A prominent tubercle is present on the squamosal plate in front of the apophysis.

Interorbit

The interorbit of *Stephanomys* is narrow, and a constriction in the middle part divides it symmetrically (Fig. 6). Conspicuous ridges can be seen outlining the boundary between the flattened supraorbital roof and the vertical orbital wall. The anterior region of the interorbit expands in front of the constricted middle part, and the ridges become parallel. A similar pattern is exhibited by *Malpaisomys* and *Stenocephalemys*.

Orbital Region

The orbits of *Stephanomys* are large. The narrow interorbit and the wide zygomatic arches leave space for relatively big eyes. A stout maxillary bone forms the ventral part of the orbit. Its anterior part is thick in *S. donnezani* and even stouter in *S. balcellsi*; *S. thaleri* exhibits an intermediate stage. The medial wall of the orbit is deeply concave. A large optical foramen can be seen in the specimen of *S. balcellsi* posterior to the level of the third molar (Fig. 8). In our specimens of *S. donnezani* the foramen is not preserved but a thin interorbital wall can be seen clearly above the third molar, indicating that the foramen was posterior to this. In other murids this foramen is usually at the level of the third molar.

Palatal Region

The incisive foramina are long and wide (Fig. 7). They occupy most of the length of the rostrum and extend beyond the anterior part of the first molars. *Malpaisomys*, *Mastomys*, and other murids exhibit a similar disposition. On the contrary, *Deomys* has short incisive foramina, which occupy half the length of the diastema nearly in front of the first molars.

The bony palate is rather long, clearly ending distal to the third molar. It is relatively wide and bordered by parallel tooth rows. The posterior palatal foramina are longer than wide, extending to the level of the second and the third molar (Fig. 7). The maxillopalatine suture is situated anterior to these teeth. Several foramina and accessory pits open in the posterior part of the bony palate. A deep pterygoid fossa is situated near the level of the choana.

Otic Region

Only isolated petrosal bones have been preserved from the otic region. They exhibit informative features about the arterial foramina. A large stapedial canal for the stapedial artery is clearly developed in the posterior part of the petrosal flange. This bone forms half of the stapedial foramen, the other half being delimited by the ectotympanic bone. The size of the stapedial foramen can be estimated on the basis of the preserved petrosal half. The carotid canal may be formed by both bones or by the ectotympanic alone, but when the petrosal bone contributes to the carotid canal, its flange is usually thin and bears no trace of the canal. In *Stephanomys* this canal could not be observed, due to the lack of the ectotympanic bone.

Comparisons

The cranial morphology of *S. donnezani*, *S. thaleri*, and *S. balcellsi* differs rather clearly, supporting the previous distinctions of the species on the basis of isolated molars. The youngest species, *S. balcellsi*, has a more robust rostrum, larger zygomatic notches, and thicker maxillary bones than *S. thaleri*, which illustrates a more or less intermediate stage between the former and *S. donnezani* (see Table I). However, the three species show a common pattern in their skull morphology, which may be summarized as follows: (1) robust anterior region, (2) high zygomatic plate, (3) wide zygomatic arch, (4) large zygomatic notch, (5) dorsal roof of the skull evenly curved (umbrella-shaped), (6) ventral branch of the zygoma starting in backward position, (7) narrow interorbit, (8) orbital margin crested, (9) backward position of the optic foramen, (10) long incisive foramen, (11) long bony palate, and (12) long palatal foramen. A set of standard measurements of the skull from the three studied species of *Stephanomys* is shown in Table II.

Table II. Some Cranial Measurements of the Three Studied *Stephanomys* Species

Measurement	*S. donnezani* (Layna, LAY MU056, UCM)	*S. thaleri* (Seynes, Montp. 1962, UM)	*S. balcellsi* (Casablanca, CAS NI6MU085, UCM)
Length of nasals	[14.36]	—	—
Length of rostrum	—	13.37	—
Breadth of nasals	4.88	4.87	9.00
Breadth of rostrum	—	8.27	8.88
Interorbital breadth	4.42	4.79	4.34
Zygomatic breadth	—	—	Ca. 21.24
Width of zygomatic plate	5.32	5.11	5.49
Length of incisive foramina	—	11.44	10.03
Length of diastema	—	11.23	11.16
Breadth of incisive foramina	—	2.86	4.20
Breadth of palatal bridge posterior to M3	—	—	5.31
Length of upper tooth row	6.13	Ca. 7.43	7.45
Width of upper M1	2.22	2.51	2.61
Estimated total length of the skull	36.6	—	41.00

Table III. Distribution of Cranial Character States in the 13 Studied Genera of Muridae

Stephanomys	2211111010?010?1
Malpaisomys	22111102100011000
Stenocephalemys	22111110000101100
Mastomys	20021100010101100
Oenomys	20021011000000100
Thamnomys	11021011000000100
Dasymys	30021010000101100
Rattus	20021010010101100
Mus	20121000000100010
Lophuromys	11001100100000000
Acomys	22021102100010010
Otomys	10021010000000100
Deomys	01000202001000000

Comparison of our reconstructions of *Stephanomys* with the single known complete skull of *Malpaisomys* (Figs. 9A and B) and numerous fragments reveals that both genera agree in most of the characters listed above, but they differ in several features. In *Malpaisomys* the anterior region is less robust, the zygomatic plate is lower, the optical foramen is not in a backward position (character 17), the pterygoid fossa is covered by a bony plate (character 7), the bony palate extends more posteriorly (character 8), and the stapedial foramen is larger (character 13) (Table III). A biometrical comparison of both genera (Fig. 10) with *Mastomys* used as a reference shows that *Malpaisomys* and *Stephanomys* share a wide zygomatic arch, narrowness of the interorbital region, a similar palatal length, and other characters already mentioned.

Another difference can be observed in the shape of the braincase (Figs. 6 and 9A and B), which is short and rounded in *Malpaisomys*, while it is probably longer and less rounded in *Stephanomys*, as far as the fragments can show. It seems that *Stephanomys* had a long braincase as in *Oenomys* or in other extant murids, while *Malpaisomys* had a round braincase, which gives its skull a gerbil-like aspect (Hutterer *et al.*, 1988).

The special cranial morphology and dental patterns of *Stephanomys* and *Malpaisomys* may be interpreted in terms of adaptations to food and habitat. Our previous suggestions for *Malpaisomys* (Boye *et al.*, 1992) may be applied to *Stephanomys*. The similarity of the skull of both genera may be correlated with the development of large eyes. Both mice may have inhabited rocky areas and possibly sheltered in rock or lava cavities and fissures. Fossils of *Stephanomys* are very abundant in karstic areas. Since *Malpaisomys* had peculiar limb proportions favorable for climbing (Boye *et al.*, 1992), the finding and analysis of postcranial remains of *Stephanomys* could be a test of our interpretation.

PHENETIC AND CLADISTIC ANALYSES OF SKULL CHARACTERS

The skull data matrix for the 13 selected taxa and the 17 characters is given in Table III. The data have been submitted to a phenetic analysis of global similarity and to several phylogenetic analyses using a parsimony approach.

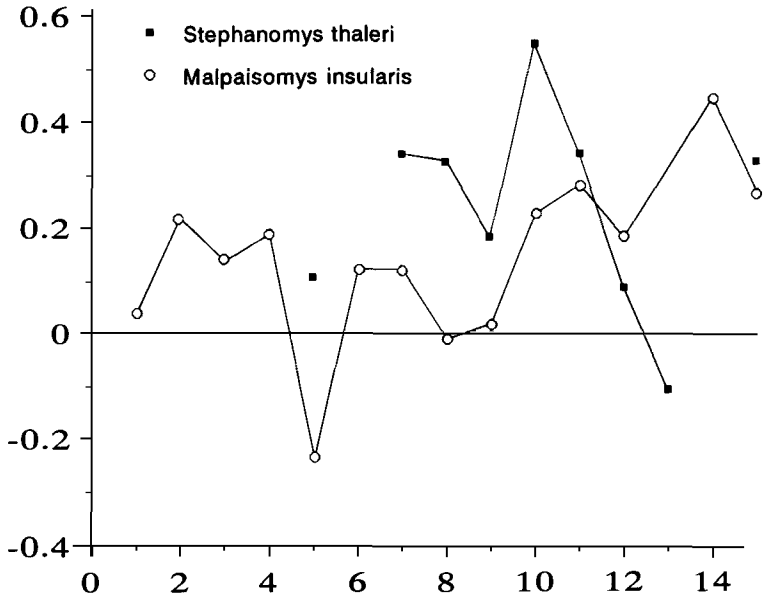

Fig. 10. Comparison of cranial measurements of *Stephanomys thaleri* and *Malpaisomys insularis*, using *Mastomys erythroleucus* as a standard. Scale of differences of logarithms [description of some measurements of Musser (1970)]: (1) greatest length of the skull; (2) zygomatic breadth; (3) breadth of braincase; (4) height of braincase; (5) interorbital breadth; (6) length of nasals; (7) breadth of zygomatic plate; (8) length of diastema; (9) length of palate; (10) length of incisive foramina; (11) breadth of incisive foramina; (12) breadth of palatal bridge at M1; (13) breadth of palatal bridge at level of upper M3; (14) length of bulla; (15) alveolar length of M1–M3.

Phenetic Analysis

The phenetic analysis arranges the studied taxa into three groups (Fig. 11). Two well-defined groups exhibit a within-group distance shorter than between-group distances. One cluster comprises the genera *Mus*, *Oenomys*, *Dasymys*, *Mastomys*, *Rattus*, *Thamnomys*, and *Otomys*. These rodents share a similar skull morphology of the *Rattus* type. The other cluster comprises the genera *Stephanomys*, *Malpaisomys*, *Stenocephalemys*, and *Acomys*, which have a different skull morphology. All four share a specialized shape of the infraorbital canal (character 2), and the first three taxa are characterized by a narrow interorbit and an evenly curved skull roof (characters 3 and 4). These 11 taxa cluster with another group made by *Deomys* and the peculiar murine *Lophuromys*.

Cladistic Analyses

The phylogenetic value of the cranial data has been tested in our study by the criteria of Hillis (1991). According to this, the skewness of the distribution of tree lengths obtained from the data set is directly related to its phylogenetic information. The curve obtained by a random sampling of 10,000 trees from the cranial data is strongly skewed, with a long left tail of short length trees (Fig. 12). Accordingly, the cranial characters have phylogenetic value.

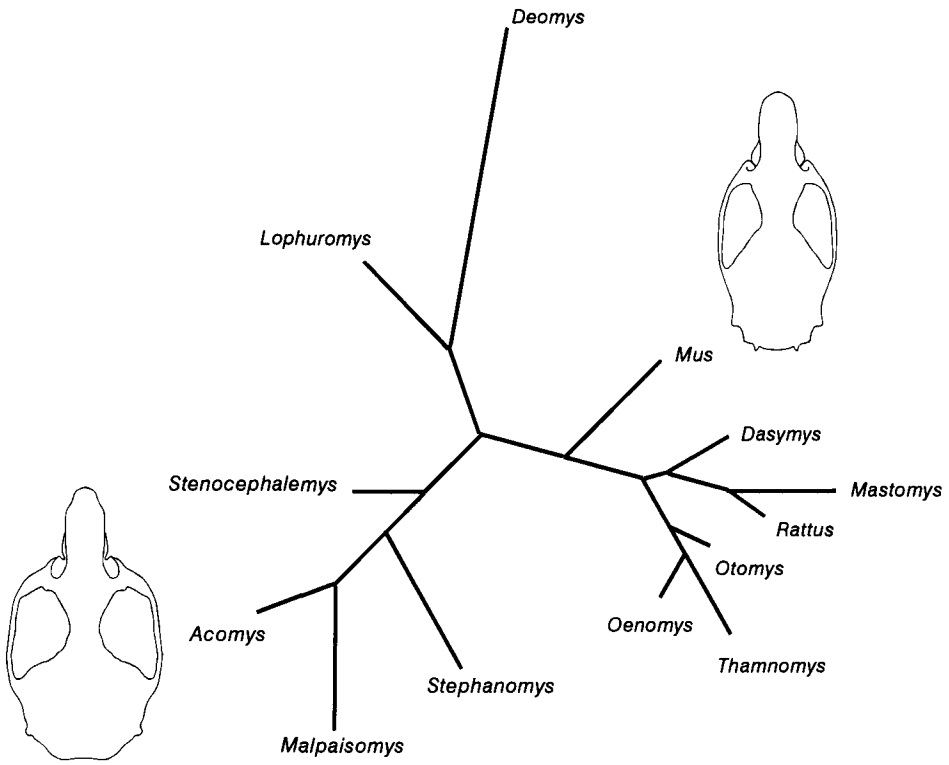

Fig. 11. Phenetic overall similarity tree (Fitch–Margoliash) of some Muridae based on skull morphology. Two main clusters are illustrated, one characterized by a *Rattus*-like skull and the other by a narrow interorbit.

Several phylogenetic analyses of the data matrix following the principle of parsimony were performed. The Lundberg method found different genera (e.g., *Mastomys*, *Mus*, and *Lophuromys*) equally probable as possible outgroups, with either unordered or ordered character states. Eighteen cladograms with 34 to 37 steps show *Stephanomys* and *Malpaisomys* near each other, clustering with *Stenocephalemys* and *Acomys*, both close to *Lophuromys* and *Deomys*, thus resembling the phenogram (Fig. 11). Accordingly, the primitive skull type of the murids examined would be the *Rattus*-like morphology.

In the case of fixed polarities, a unique tree with 44 steps (not shown) is found using HENNIG86. The root is located by inserting a hypothetical ancestor having all the primitive states of characters. *Deomys* is then separated from the rest of the taxa, its peculiar skull features indicating a divergent evolution. In this cladogram *Malpaisomys* clusters with *Acomys*, then *Stephanomys* and *Stenocephalemys*. The grouping of *Malpaisomys* and *Acomys*, defined by at least two synapomorphies (characters 8 and 13), agrees with our earlier interpretation (Hutterer *et al.*, 1988). The search using PAUP produced nine trees of shorter length (40 steps; see consensus tree in Fig. 13, left), essentially similar to that found by HENNIG86.

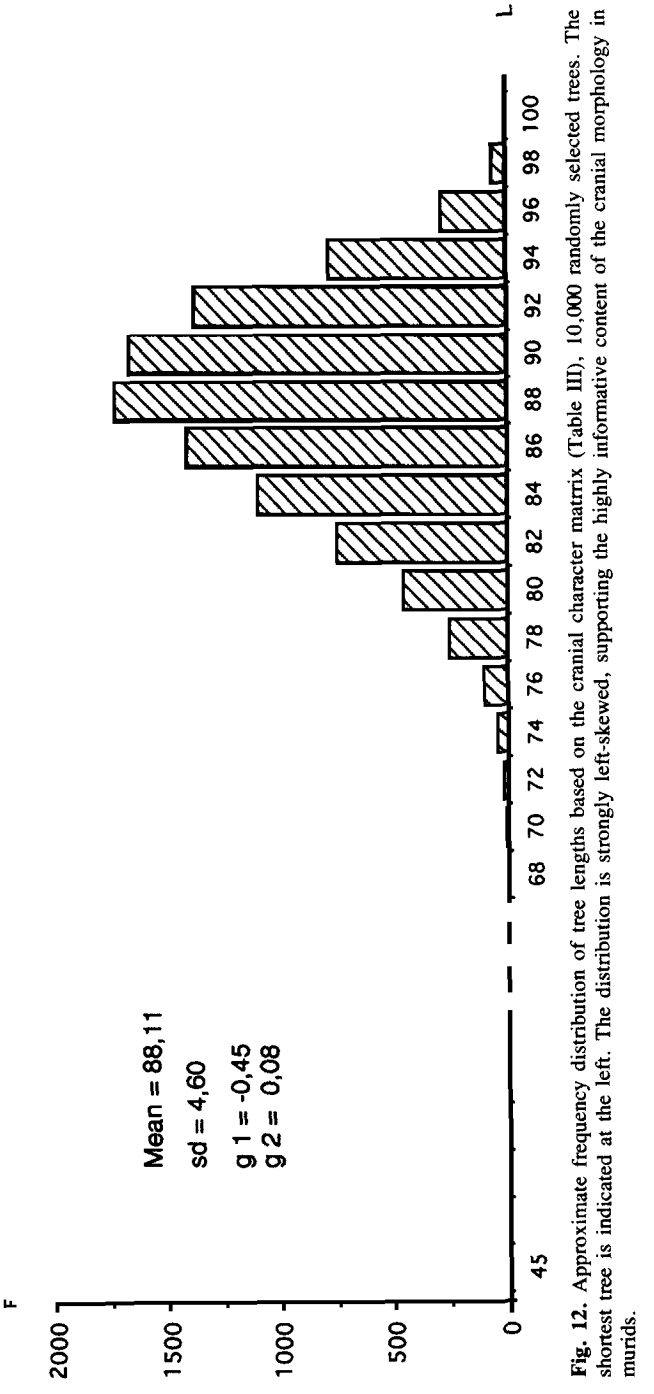

Fig. 12. Approximate frequency distribution of tree lengths based on the cranial character matrrix (Table III), 10,000 randomly selected trees. The shortest tree is indicated at the left. The distribution is strongly left-skewed, supporting the highly informative content of the cranial morphology in murids.

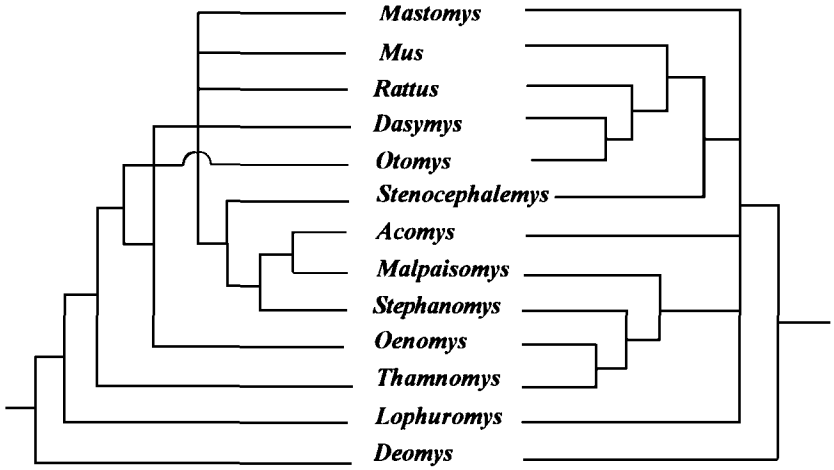

Fig. 13. Left: Consensus tree of nine equally parsimonious cladograms using PAUP (40 steps), based on ordered states of cranial characters; *Deomys* fixed as outgroup (statistics of the tree: normalized consensus fork index CF = 0.73; Mickevich's consensus information MCI = 0.58). Right: Consensus tree of five equally parsimonious cladograms (54 steps), based on ordered states of dental characters; Lundberg method for choosing the outgroup (statistics of the tree: CF = 0.72, MCI = 0.47).

The distribution of cranial characters has consistency indices (CI) ranging from 0.66 to 0.57, indicating a large number of homoplasies. The narrow interorbital area outlined by crests (skull character 4) is shared by *Stephanomys*, *Malpaisomys*, and *Stenocephalemys* but not by *Acomys*, so a parallel evolution may have occurred (Fig. 13, left). Similarly, other morphological traits may have been subject to parallel evolution, such as the ovoid shape of the infraorbital canal (character 2), the umbrella-shaped profile of the skull (character 3), and the insertion of the ventral branch of the zygomatic arch at the level of the first molar (character 15). This results in a relatively high number of shorter trees, with no one cluster shared by all of them. That may be compared with the different grouping based on the dental character distribution (Fig. 13, right).

PHENETIC AND CLADISTIC ANALYSES OF DENTAL CHARACTERS

The genus *Stephanomys* and the genera *Malpaisomys*, *Oenomys*, and *Thamnomys* share some dental characters which have been used to define "stephanodonty." This term was coined by Schaub (1938) to describe a special pattern of the upper molars where the five posterior main cusps are connected in a crown-shaped ring (*stephano* = crown). Connections between the anterior cusps and the latter ones define a more advanced state of stephanodonty. In the stephanodont Murinae, the lower teeth show a longitudinal, central crest linking the main pairs of cusps. Figure 14 shows the stephanodont molars of *Stephanomys thaleri* n. sp. (holotype). The phylogenetic significance of stephanodonty needs to be analyzed in relation with other features of the Murinae. Table IV gives the data matrix used for the dental character analyses.

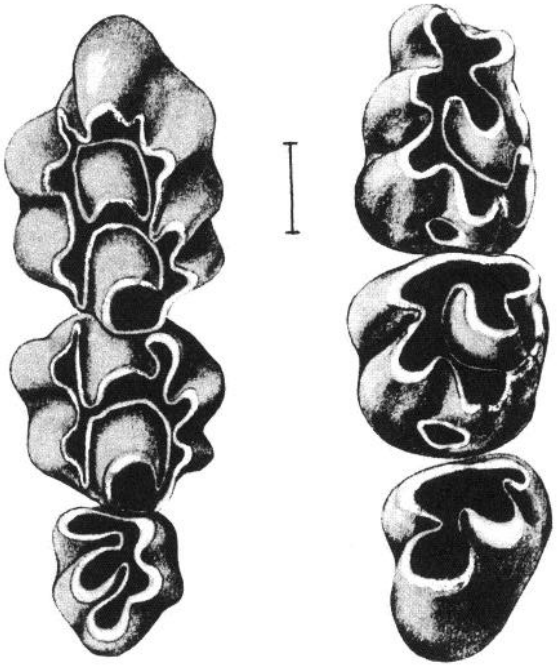

Fig. 14. Dentition of *Stephanomys thaleri* n. sp. from Seynes (Gard, France), showing complete stephanodonty. Left: Upper M1–M3 (UM 07). Right: Lower m1–m3 (holotype, UM 47).

Table IV. Distribution of Dental Character States in the 13 Studied Genera of Muridae

Stephanomys	01010100222220101200111
Malpaisomys	00011000121121111000111
Stenocephalemys	00011000000020011010111
Mastomys	00011000000020001000101
Oenomys	00111000211221111110101
Thamnomys	00112000211200001110101
Dasymys	12112010000022210010111
Rattus	00112000000020010011111
Mus	00011000000020012011111
Lophuromys	00111000000010011000100
Acomys	00010000000120111000100
Otomys	12112001000022210011111
Deomys	00000000000000011010000

Phenetic Analysis

The phenetic analysis based on dental morphology (Fig. 15) gives a phenogram with taxa organized along four main axes. One is made by the taxa with a bunodont, less specialized crown pattern, such as *Mastomys*, *Stenocephalemys*, *Mus*, and *Rattus*.

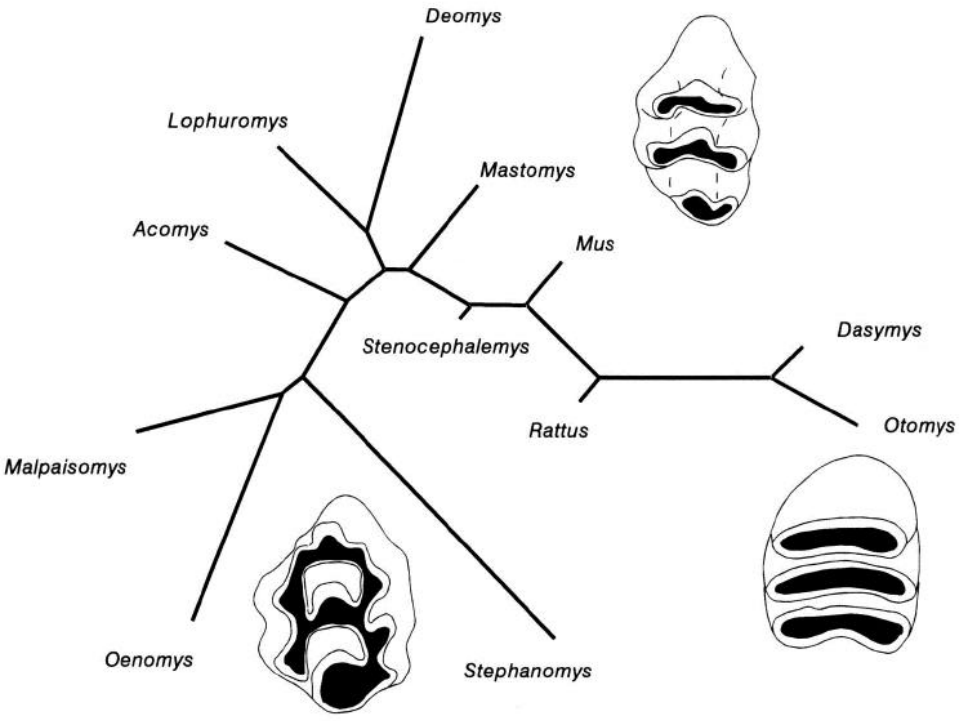

Fig. 15. Phenetic overall similarity tree (Fitch–Margoliash) of the murids examined, based on dental morphology. Three main dental patterns are illustrated: stephanodont at the bottom, unspecialized at the top, and lophodont at the right (black areas represent dentine; white areas, enamel).

Another is made by the murids with a lophodont pattern (*Dasymys* and *Otomys*), connected to the latter taxa through *Rattus*. The third axis groups the stephanodont murids (*Stephanomys*, *Oenomys*, *Thamnomys*, and *Malpaisomys*), linked to the less specialized taxa through *Acomys*. Finally, the fourth axis is made by *Lophuromys* and *Deomys*, which are situated as far from each other as they are from the rest of the taxa.

Cladistic Analyses

Using unordered dental character states, seven minimal-length trees were obtained (48 steps). The Lundberg method for the search of an outgroup gives *Malpaisomys* as a possible ancestor. The other stephanodont taxa appear near the root. This suggests that the asserted dental polarities are reversed, i.e., evolution from the more complex (e.g., stephanodont) to the more simple dental pattern (e.g., bunodont) is more parsimonious. With ordered character states, *Deomys* was the only outgroup selected by the Lundberg option (five trees of 54 steps; consensus tree in Fig. 13, right). All five cladograms have generally two main clusters: one with the four stephanodont taxa (*Stephanomys*, *Malpaisomys*, *Oenomys*, and *Thamnomys*) and the other with the remaining genera. Homoplasies are frequent in dental characters (CI = 0.54). The taxa with a *Rattus*-like skull show differently derived tooth morphologies. In conclusion, the results from the

cladistic analysis of dental characters agree in the clustering of taxa but give two conflicting hypotheses of the evolutionary polarity. In one case, stephanodonty would be a primitive character; in the other case, it would be a synapomorphy of four geographically and chronologically distant genera. *Deomys* appears as a plausible outgroup in this case, but it does not in the case of cranial character analysis.

Taxonomic incongruence results from the comparison of both data sets (Fig. 13). No informative consensus tree can be obtained from mixing the two partial analyses [partitioned evidence (see Hillis, 1987)]. It can be tested only by using dental and cranial characters combined in one matrix (Kluge and Wolf, 1993).

CRANIAL AND DENTAL CHARACTERS COMBINED

We analyzed the combined data matrix of all 40 cranial and dental characters in different ways. With unordered character states, a tie among different possible outgroups, such as *Mastomys*, *Mus*, and *Stenocephalemys*, was encountered by the Lundberg method. Alternatively, the Midpoint method rooted the tree between *Lophuromys* and *Deomys* on one side and the remaining taxa on the other side, meaning that these two former taxa are phylogenetically far from the rest (patristic distance). The 13 shortest cladograms (99 steps) have several topological similarities: *Stephanomys* and *Malpaisomys* are sister taxa and group with *Acomys*. Another cluster is made by *Oenomys* + *Thamnomys*. However, the latter taxa appear connected with the first cluster (forming the clade of the stephanodont murines) in some trees but connected with the group with a *Rattus*-like skull (*Rattus* + (*Dasymus* + *Otomys*)) in the other trees. Therefore, the consensus tree shows a polytomy with all these taxa. The taxonomic congruence using unordered characters is thus very low, and consequently convergences in teeth or skull characters cannot be discriminated.

With ordered characters or fixed polarities, the Lundberg method selected *Deomys* as the only outgroup and two equally parsimonious trees were obtained (106 steps; CI = 0.54; Fig. 16). The four stephanodont taxa are grouped, *Acomys* being the sister group. *Stephanomys* branches either with *Malpaisomys* or with the cluster *Oenomys* + *Thamnomys*. The ordered option gives a higher taxonomic congruence, indicating that convergences of skull characters are more probable than those of dental characters.

Thus, the combined cranial and dental characters support the cluster of *Stephanomys* + *Malpaisomys* and *Acomys*, shared by the 26 shortest trees with unordered character states and by the 2 shortest trees with fixed polarities. This result supports our first interpretation of *Malpaisomys* origins (Fig. 1, left).

DISCUSSION AND CONCLUSIONS

The taxonomic position of *Stephanomys*, far apart from any other murid, is suggested clearly by both cranial and dental phenetic analyses. In contrast, cladistic analyses of the cranial and dental morphological characters shared by *Stephanomys* and *Malpaisomys* support a close phylogenetic relationship of these genera. Some of these characters (robustness, umbrella-shaped roof, narrow interorbit, large orbits with crested margin) can be interpreted as functional features for a similar mode of life, both genera being linked to a rocky landscape. A phylogenetic relationship is moreover suggested

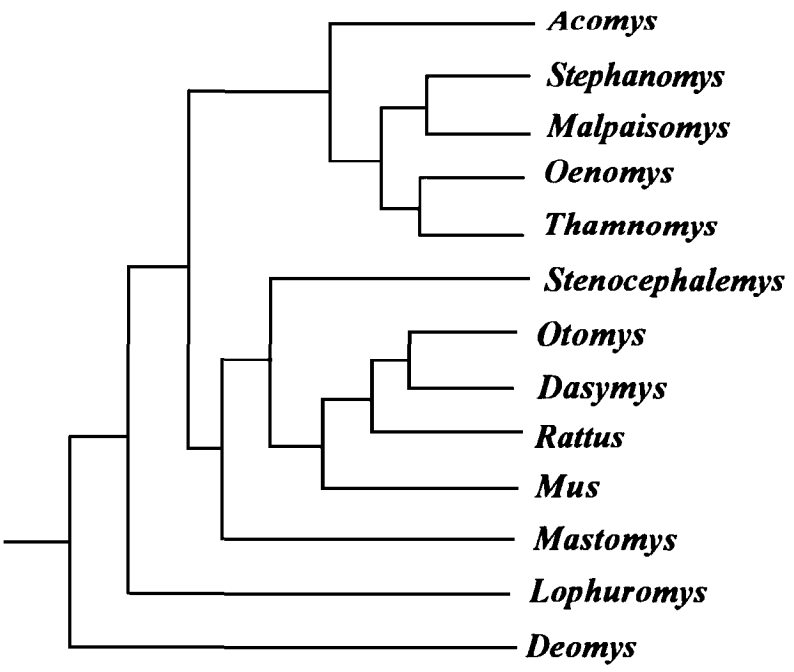

Fig. 16. One of the two most parsimonious cladograms using PAUP (106 steps), based on ordered cranial and dental characters combined, using the Lundberg method for search of the outgroup.

by other characters such as the long incisive foramen, long bony palate, and dental stephanodonty. Differences are observed in the shape of the braincase, short and rounded (gerbil-like) in *Malpaisomys* while probably elongated in *Stephanomys*, and also in the rostrum, bony palate, optic and stapedial foramen, and less developed stephanodont teeth, indicating an important morphological divergence between them.

The close phylogenetic relationship between *Stephanomys* and *Malpaisomys* is in agreement with all analyses of cranial, dental, and combined characters. Nevertheless, the lack of congruence of the cladograms obtained by different methods and sets of characters precludes a conclusive hypothesis about the phylogenetic relationships between *Malpaisomys* and *Acomys*. Comparing phylogenies based on partial evidence (dental characters separately; Fig. 13, right), *Acomys* branches with other murines including *Malpaisomys* and *Mus* in a basal polytomy. Conversely, analyses of the cranial and combined characters support the monophyly of *Stephanomys*, *Malpaisomys*, and *Acomys* within the Murinae, thus conforming to our initial interpretation of the relationship between *Acomys* and *Malpaisomys* (Hutterer *et al.*, 1988, Fig. 1a). The alternative hypothesis, based on biochemical data (Montgelard, 1992, Fig. 1b), disagrees with any parsimonious phylogeny based on morphological data.

On the other hand, our results corroborate the conclusions from Chevret *et al.* (1993a) that *Otomys* belongs to the Murinae and not to a separate subfamily Otomyinae, as widely accepted (Musser and Carleton, 1993). An early differentiation of *Rattus* and *Mus*, as advocated by several authors (Jacobs, 1978; Jacobs and Pilbeam, 1980; Jaeger

et al., 1986; Catzeflis, 1990), is not supported by any of the 93 most parsimonious trees obtained in our analyses.

Discrepancies between phylogenetic hypotheses based on different character sets have been encountered frequently in the literature (Mickevitch, 1978; Rieppel, 1989; Swofford, 1991; Wheeler, 1991; Luckett and Hartenberger, 1993; Kluge and Wolf, 1993; Denys *et al.*, 1995). Our analyses offer an informative example for such discrepancies. In the present case we assume that cranial and dental morphology in rodents may follow different evolutionary pathways. When teeth are concerned, a monophyletic clade including *Stephanomys*, *Malpaisomys*, *Oenomys*, and *Thamnomys* is recognized in all the analyses, defined by the so-called stephanodont morphology. However, no parsimonious trees based on skull characters support this monophyletic clade. This illustrates a case of mosaic evolution for these taxa.

This lack of correlation between the cranial and the dental characters is enlightened by the discovery of the *Stephanomys* skulls. With the teeth only, the genus would be considered to be closer to the *Oenomys* + *Thamnomys* clade, and a *Rattus*-like skull would be inferred for *Stephanomys*. This illustrates the importance of new fossil findings, which may show unexpected combinations of characters.

APPENDIX

Taxonomic Comments on the Genus *Stephanomys*

The names *Stephanomys* "*michauxi*," *S.* "*medius*," *S.* "*thaleri*," and *S.* "*progressus*" were proposed by Cordy (1976) in an unpublished manuscript and are still formally *nomina nuda*. They are thus unavailable, although some of them have been widely used. *S.* "*michauxi*" is a synonym of *S. ramblensis*, *S.* "*medius*" has been renamed *S. donnezani cordii* by Ruiz Bustos (1986), *S.* "*progessus*" is a synonym of *S. balcellsi*. See Results for further comments and corrections. The following species have been described to date.

Late Miocene

S. ramblensis Van der Weerd, 1976; *Utrecht Micropal. Bull. Spec. Publ.* **2:** 67; Rambla de Valdecebro 3, Teruel, Spain

S. stadii Mein and Michaux, 1979; *Geobios* **12:** 482; Cucuron, Vaucluse, France

Latest Miocene–Earliest Pliocene

S. debruijni De Giuli, 1989; *Bol. Soc. Pal. Ital.* **28:** 200; Brisighella, Faenza, Italy

S. dubari Aguilar, Michaux, Bachelet, Calvet, and Faillat, 1991; *Paleovertebrata* **20:** 153; Castelnou 3, Pyrénées Orientales, France

S. numidicus Coiffait, Coiffait, and Jaeger, 1985; *Proc. Kon. Neder. Akad. Wetensch. B* **88:** 169; Argoub Kemellal, Constantine, Algeria

Pliocene

S. amplius Ruiz Bustos, 1986; *Paleomammalia* **1:** 16; Moreda, Granada, Spain

S. ballcelsi Gmelig Meyling and Michaux, 1973; *C.R. Acad. Sci. Paris D* **277:** 1442; Islas Medas, Girona, Spain [=*S.* "*progressus*" Cordy, 1976 *nomen nudum*]

S. calveti Bachelet and Castillo Ruiz, 1990; *C.R. Acad. Sci. Paris II* **311:** 494; Plà de la Ville, Pyrénées Orientales, France

S. donnezani Déperet, 1890; *Mém. Soc. Geol. France Paléont.* **3:** 50; Perpignan, Pyrénées Orientales, France

S. d. cordii Ruiz Bustos, 1986; *Paleomammalia* **1:** 13 [=*S. "medius"* Cordy, 1976 *nomen nudum*]; Alcoy, Alicante, Spain

S. d. adroveri Ruiz Bustos, 1986; *Paleomammalia* **1:** 13; Aldehuela, Teruel, Spain

S. laynensis Ruiz Bustos, 1986; *Paleomammalia* **1:** 17; Layna, Soria, Spain

S. margaritae Adrover, 1986; "Nuevas faunas de roedores. . . ," Inst. Est. Turolenses, p. 235; La Calera II, Teruel, Spain

S. minor Gmelig Meyling and Michaux, 1973; *C.R. Acad. Si. Paris D* **277:** 1441; Moreda, Granada, Spain

S. prietaensis Aguilar, Michaux, Delannoy, and Guendon, 1993; *Scripta Geol.* **103:** 10; Alozaina, Málaga, Spain

S. thaleri n. sp. Seynes (Gard, France); this paper

S. vandeweerdi Adrover, 1986; "Nuevas faunas de roedores. . . ," Inst. Est. Turolenses, p. 243; Orrios 3, Teruel, Spain

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